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What are ecological mechanisms? Suggestions for a fine-grained description of causal mechanisms in invasion ecology

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Abstract
Invasion ecology addresses the spread of species outside of their native ranges. A central aim of this field is to find mechanistic explanations for why species are able to establish and spread in an area in which they did not evolve. Usually it remains unclear, however, what exactly is meant by 'mechanistic explanation' or 'mechanism'. The paper argues that the field can benefit from the philosophical discussion of what a mechanism is. Based on conceptions of mechanisms as processes in concrete systems, causal mechanisms can be defined as one type of mechanism, representing recurring networks of causal relationships. With the example of a well-known hypothesized mechanism in invasion ecology, namely *enemy release*, the paper demonstrates how such causal mechanisms can be depicted as causal network diagrams. This approach could facilitate the development of step-by-step explanations, enhance clear argumentation and allow for more precise linkage of empirical tests to theory. Challenges to assessing the empirical relevance of hypothesized mechanisms are discussed, and suggestions are made concerning how the proposed approach could help in overcoming some of them.

Keywords Invasion ecology · Mechanistic explanation · Hierarchy-of-hypotheses approach · Causal network graphs · Multicausality · Connecting empiricism and theory

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Introduction

Examples for invasive species abound (CABI 2020). Plants are traded worldwide as garden plants; many of them escape from the gardens and spread in the wild. Non-native fish are introduced for angling or commercial fishing, and often start to proliferate and spread in the new range. Further, many organisms are transported as hitchhikers on traded goods to areas in which they subsequently establish and spread. The number of species that start spreading in areas in which they did not occur previously is constantly rising (Seebens et al. 2017), and many of these species cause economic or health problems, or threaten native biodiversity (IPBES 2019; Pyšek et al. 2020b).

Accordingly, there is a lively research area trying to find ways for explaining, predicting, and controlling invasion processes: invasion ecology. Here, the goal of research very often is to reveal the mechanisms underlying species invasions (e.g. Gurevitch et al. 2011; Pyšek et al. 2020a). However, what exactly it means to reveal a mechanism is rarely discussed (Raerinne 2011). In philosophy, on the contrary, there are lively discussions on what a mechanism is, and how it can be studied in biology.

This article will discuss in which respect the philosophical debate on mechanisms can be useful for ecology, choosing invasion ecology as an example. In invasion ecology, much research is driven by one overarching question, which is: “Which factors allow species to establish and spread outside of their native range?” (Lowry et al. 2013). The field is consequently dominated by a set of major hypotheses suggesting possible answers to this question (Catford et al. 2009; Enders et al. 2020; Jeschke and Heger 2018). Many of these major hypotheses can be interpreted as suggesting mechanisms that may drive species invasions (Küffer et al. 2013), and are therefore prime examples for discussing what it could mean to describe mechanisms in ecology.

In the following sections, I will first provide more background information on invasion ecology to familiarize readers with this case study. I will introduce recent work that summarizes major hypotheses in this field. Next, I will discuss in which respects the current philosophic discussions on mechanisms may be helpful for ecology in general. Coming back to the case study, I will then develop a suggestion for how to enhance research practice, based on one specific notion of ‘mechanism’ and using the so-called enemy release hypothesis as an example. The last section will discuss challenges connected to assessing the empirical relevance of mechanisms, and will indicate possible solutions.

Introducing the case study: the search for mechanisms in invasion ecology

Given the basic conception that species evolve in close interaction with their biotic and abiotic environment, it is striking that invasive species get along very well in environments in which they did not evolve, sometimes even growing and reproducing more effectively than in their native environments (Parker et al. 2013). Over the years, many ideas have been developed in the field on which factors may explain such observations (see e.g. Catford et al. 2009; Enders et al. 2020; Hui and Richardson 2017; Küffer et al. 2013; Lowry et al. 2013; Richardson 2011).

With the aim of providing an overview of existing knowledge in invasion ecology, a recent edited volume focuses on twelve broad hypotheses that have been proposed for explaining species invasions (Jeschke and Heger 2018). For each hypothesis, an author team conducted a literature analysis to assess whether empirical evidence corroborates or rejects it. Based on the identified empirical tests, hierarchical representations of the hypotheses were created applying the hierarchy-of-hypotheses (HoH) approach (Heger et al. 2021). These twelve hypotheses are formulated as broad, rather general ideas, whereas the single empirical studies each address specific aspects of the respective hypotheses. The HoH approach can account for this circumstance, and offers the opportunity to represent the resulting complexity. In addition to the single chapters presenting empirically evaluated HoHs, Enders and Jeschke (2018) developed a network connecting the twelve hypotheses according to conceptual closeness. The hierarchical network for invasion biology (HNI), combining the hypotheses network with the twelve HoHs, is published as an interactive online tool at https://hi-knowledge.org/ (Jeschke et al. 2020). An enlarged version of the network (Enders et al. 2020) is accessible there as well.

The HNI provides a graphical representation of major ideas on which factors allow species to establish and spread outside of their native ranges, and presents a graphical summary of the available evidence. Hypotheses that received broad support are color-coded in green, and those that were mainly rejected in red. Clicking on a hypothesis in the online version reveals the respective HoH, where the same color coding is applied to the lower levels of the hierarchy, displaying the level of evidence for the more specific formulations of the major hypothesis.

The HNI is an important step towards developing novel ways for summarizing existing knowledge on biological invasions. However, if looking for explanations on why species are able to establish and spread outside of their native range, this summary may still leave the user unsatisfied. For example, the so-called *enemy release hypothesis* states that the "absence of enemies is a cause of invasion success" (Heger and Jeschke 2014; Keane and Crawley 2002). Especially to someone not knowledgeable about ecology or biological invasions, this statement only provides a rough answer for the question "How does it work?" In Heger and Jeschke (2018b), this major hypothesis is sub-divided into two lower-level hypotheses: (a) invaders are released from enemies, and (b) invaders show enhanced performance (e.g. enhanced growth, more offspring) if released from enemies. These sub-hypotheses address two aspects of the general claim. However, someone looking to find possible explanations for why a species is a successful invader might still ask: "But how does this work? Which processes could lead to a lack of enemies in the invaded range? What are the variables involved in an invasive species' success, and how do they change in the absence of enemies?".

Providing answers to these questions requires to go into more detail concerning the suggested causal processes leading to a release from enemies or to enhanced performance of the invaders, thus moving from describing patterns to a 'mechanistic explanation'. The discovery of mechanisms that produce observed patterns is commonly viewed as a central goal of research in ecology (McGill and Nekola 2010). What exactly a 'mechanistic explanation' or a 'mechanism' is, is usually taken for granted in respective ecological papers (e.g. Helmuth et al. 2005). However, taking a look at models in macroecology, Connolly et al. (2017) point out that the usage of these terms in ecology is inconsistent, and that respective clarifications are overdue. According to these authors, the use of the term 'mechanistic models' without clear characterization of their difference to and advantage over other models has led to an underestimation of their usefulness for ecological research. I agree with them that a clarification of the term 'mechanism' has the potential to enhance scientific workflows and to strengthen the link between theory and data.

New mechanical philosophy and possible applications in ecology

During the last two decades, a philosophical research program emerged around the concept of the 'mechanism' (Levy 2013; Nicholson 2012). Looking into common research practices in biology, several groups of philosophers identified 'mechanisms' as important components of scientific explanations (Bechtel 2006; Craver and Darden 2013; Glennan 2002; Machamer et al. 2000). This school of thought has often been named the 'new mechanical philosophy' (del Solar et al. 2019). Also prior to these rather recent advances, mechanisms have been regarded as central to scientific inquiry by some philosophers (e.g. Bunge 1997). Taken together, diverse views have been published on how mechanisms can be defined, and which role they have in scientific reasoning. Several recent publications discuss ways for systematizing the underlying ideas (del Solar et al. 2019; Levy 2013; Nicholson 2012).

The new mechanical philosophy commonly considers mechanisms as complex objects or systems with a specific composition and interactions or activities (del Solar et al. 2019; Machamer et al. 2000). This view seems to match the usage of this term in cell biology, molecular biology and neuroscience, and it has been suggested that it applies to ecology as well (Pâslaru 2018; Raerinne 2011). Other authors have argued that in ecological research, mechanisms are not commonly regarded as real complex systems with entities and activities (Potochnik 2020). Based on a nicely worked-out example taken from ecological literature, del Solar et al. (2019) have shown that in ecology, the term mechanism rather refers to processes, not objects or systems. The authors argue that therefore, a conception of mechanism as suggested by the philosopher Bunge might be more helpful. Bunge (1997, p. 414) defines, having social sciences in mind: "a mechanism is a process in a concrete system, such that it is capable of bringing about or preventing some change in the system as a whole or in some of its subsystems". With this contribution, I would like to strengthen this view on mechanisms in ecology. Even if it remains to be discussed whether 'concrete system' is a useful concept in ecological contexts, judging from my own experience I agree with del Solar et al. (2019) that Bunge's definition matches the current usage of the term in ecology very well. Also, thinking of mechanisms as complex systems with entities and activities might work at the level of individuals (see Pâslaru 2018 for an example), but for higher level systems, following this conception would bring about serious challenges e.g. in delineating meaningful stable entities or compartments.

In the following, I will focus on *causal mechanisms* as important elements of explanation in invasion ecology, thus leaving aside other forms of mechanisms (as e.g. probabilistic and mixed mechanisms in the sense of Bunge 2004). A useful definition is provided by Nicholson (2012, p. 153): "Causal mechanism: a step-by-step explanation of the mode of operation of a causal process that gives rise to a phenomenon of interest". It is helpful to additionally characterize causal mechanisms as distinguished from *singular causal effects*. Pointing to some direct cause of an observed effect (e.g. the death of a specific plant due to a fungal disease, mediated by the fungus releasing a substance that is toxic for the plant) provides an explanation; but I suggest that ecologists would not call this a mechanism. A helpful suggestion is that the search for mechanisms rather corresponds to the search for *causal patterns* (Potochnik 2020). Causal patterns are regularities in causal dependencies. To describe causal patterns means to describe causal relationships *plus* their scope or extent, i.e. the range of circumstances in which similar causal dependencies occur (Potochnik 2020, p. 24). Taken together, I suggest that describing mechanisms in ecology means providing a step-by-step explanation of how causal relationships that happen recurringly under certain circumstances give rise to the phenomenon of interest.

Equipped with these clarifications concerning what the term 'mechanism' could mean in ecology, I will now develop a suggestion for how to advance research practice in invasion ecology. This suggestion aims at stimulating efforts in this field for improving clarity in argumentation, and at providing a method that encourages opening 'black boxes', i.e. looking for step-by-step explanations. I suggest that in this way, hidden assumptions can be made explicit and thus made available for empirical tests. Integrating the detailed description of hypothesized mechanisms into scientific workflows has the potential to lead to deeper understanding of biological invasions, and to improved capacities for making predictions and developing management solutions.

Causal network diagrams as tools for describing mechanisms

The enemy release hypothesis is a very well known, if not the best-known hypothesis in invasion ecology (Enders et al. 2018). In the Introduction, I noted that it suggests only a very rough answer to the question "How does it work?". To improve this

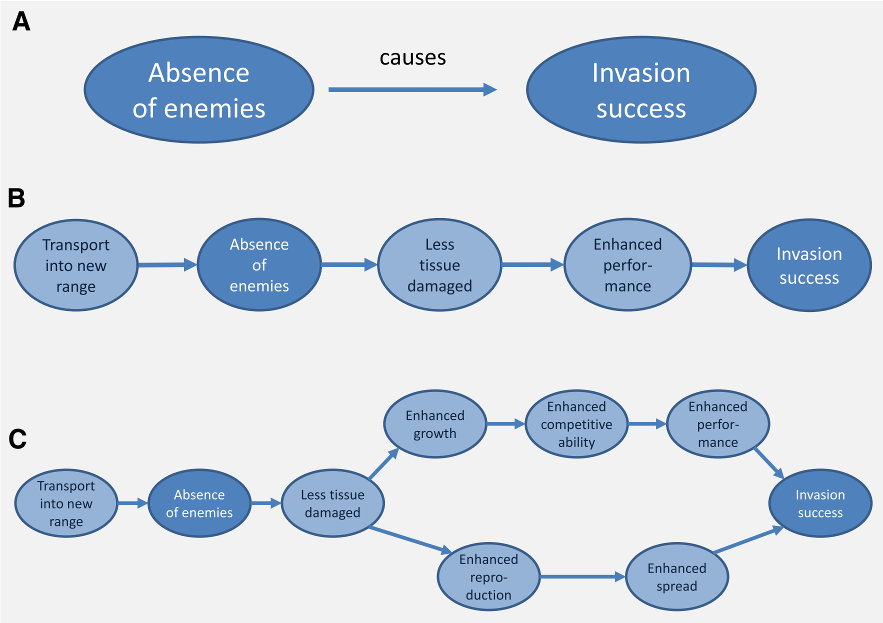

Fig. 1 Assumptions underlying common conceptions of the enemy release hypothesis, depicted as a causal network diagram for the case of plant invasions. **a** The general version of the hypothesis is similar to a black box, i.e. detailed causes are not given explicitly. **b, c** Causal network diagrams could be used to describe the hypothesized underlying mechanism in greater detail. Light blue nodes show added information. Arrows depict hypothesized causal relationships

situation, it would be helpful to describe the hypothesized underlying causal mechanism in the sense defined above, i.e. to describe a set of successive causal relationships that is expected to occur as consistent pattern. In the case of the enemy release hypothesis, experts in the field will probably have various plausible ideas in mind for what may cause an absence of enemies and how it may affect species performance; usually, however, these ideas are not made explicit in their full complexity.

The enemy release hypothesis in its general version suggests that "absence of enemies is a cause of invasion success" (Fig. 1a). The underlying idea here is that upon transportation into a new region (e.g. as garden plant, or hitchhiker on some transported good), enemies like predators or parasites are left behind, and in the new range, potential enemies do not recognize the novel organism as potential prey or host. This absence of enemies in turn leads, in case of alien plants, to less tissue being lost to herbivores or parasites, allowing an enhancement of performance and thus invasion success; in case of animals, fewer individuals will be killed by predators or suffer from parasites, also increasing invasion success of the alien population (for a discussion of negative causation in ecology see e.g. del Solar et al. 2019). Figure 1b shows these additional assumptions implied in the general formulation in the form of a causal chain diagram. In Fig. 1c, more hypothetical causal relationships are added, showing that a decrease in damage imposed by enemies could lead to enhanced growth of the invader (e.g. van der Putten et al. 2007), causing competitive advantage and thus enhanced performance (Eschtruth and Battles 2009), or to enhanced reproduction (Williams et al. 2010) and subsequently increased population growth rate (Roy et al. 2011), facilitating the spread of the species within the new range. Enhanced performance of individuals as well as enhanced spread in this conception can both be causes for invasion success.

Causal network diagrams like the one suggested in Fig. 1c could become valuable tools for describing and visualizing mechanisms in ecology. Above, I suggested that describing mechanisms in ecology means providing a step-by-step explanation of how causal relationships that happen recurringly under certain circumstances give rise to the phenomenon of interest. Causal network diagrams could be used to aid this description, by enhancing explicit formulation of hypothesized or observed causal relationships, and by providing a visual representation of the assumed or discovered relationships. More advanced versions could be developed describing the strength of relationships as well, or allowing for bidirectionality.

Similar network diagrams are gaining importance in ecology in combination with the statistical method of structural equation modelling (Grace et al. 2010), but they are not common yet as stand-alone method to allow conceptual clarifications (see also Grace et al. 2014). In addition to the obvious benefits of triggering precise argumentation, depicting hypothesized mechanisms as causal network diagrams would bring about the advantage that shifts in the meaning of a hypothesis would become explicit. In ecology, as is probably the case in other scientific fields as well, the original conjectures that have led to the formulation of a hypothesis often are not carried along with the terms. Even if the words naming a hypothesis remain the same over time, the underlying ideas may change considerably (Grace et al. 2014). This

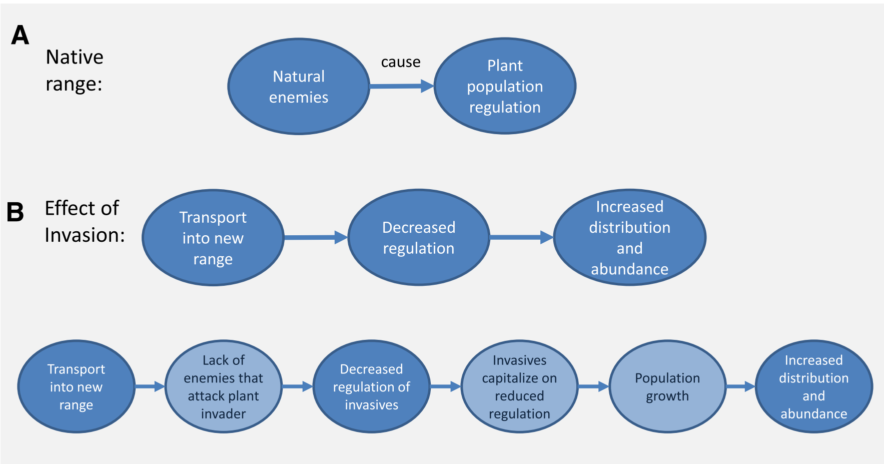

Fig. 2 Original formulation of the enemy release hypothesis, translated into a causal network diagram. **a** In its original version suggested by Keane and Crawley (2002), the enemy release hypothesis consisted of a set of assumptions about plant species in their native range and processes occurring during the course of the invasion. **b** Besides this general formulation of the hypothesis, additional assumptions about the mechanism were given in the main text (added here in light blue). Arrows depict hypothesized causal relationships

is true also for the enemy release hypothesis. Figure 1 depicts the assumptions that have been addressed by empirical studies according to a review in 2018 (Heger and Jeschke 2018b); and Fig. 2 summarizes the mechanism as hypothesized in Keane and Crawley (2002), which is commonly referred to as the original publication for the enemy release hypothesis. The prevailing conception of the hypothesis deviates from the original one in many respects, and the implications of these differences for invasion ecology would deserve further study.

A second major advantage of describing hypothesized mechanisms with causal network diagrams is the resulting option for a more precise linkage of empirical tests to the hypothesized mechanism. For example, the majority of empirical tests assessed in the 2018 review study focused on the question whether invaders are released from enemies, and only a minority of studies took the more comprehensive approach of studying whether invaders actually show enhanced performance if released from enemies (Heger and Jeschke 2018b). Moreover, empirical evidence tends to corroborate the claim that upon arrival in a new range, species are released from enemies, but tends to contradict the suggestion that released invaders show enhanced performance (Heger and Jeschke 2018b). These findings demonstrate the importance of clarifying which aspect of a general claim an empirical test actually focuses on.

Previously, the hierarchy-of-hypotheses approach has been suggested to accommodate this necessity (Heger et al. 2021; Jeschke and Heger 2018). A recent criticism, however, points out that until now, this method did not account for differences between causal and non-causal claims (Schurz 2021). A promising way forward could be to combine the hierarchy-of-hypotheses approach with causal network diagrams. For example, those hypotheses that amount to causal claims could be depicted as causal network diagrams; and hypotheses that do not claim causal relationships, but suggest the recurring occurrence of correlations, could be marked as such for example by the naming them ‘correlational hypotheses’. Sub-hypotheses of causal hypotheses developed by specialization or decomposition (Heger et al. 2021) could then be depicted as causal network diagrams as well, with the graphs getting more and more fine-grained the more specific the sub-hypothesis is.

In biological systems, complex causal relations abound, and multiple causes are often active at the same time. Currently, there is a tendency for over-simplification in biology, and approaches are needed that allow for overcoming these tendencies and explicitly considering such complex causal patterns (Potochnik 2020). Causal network diagrams could proof useful in this respect. The figures above are meant as a first proof of concept; in a next step, complexity could be added for example by adding ‘absence of competitors’ or other factors that may be caused by transportation to a new range into the diagram in Fig. 1b (cf. Schurz 2021, p. 355). Focusing in on the relationship of plant diversity and productivity, a recent study illustrates how causal network diagrams can help analyzing multicausality in ecology (Parreño et al. 2021). Using simple network diagrams, the authors visualize possible causal links of the four factors nutrients, light, biodiversity and biomass production, and demonstrate that current hypotheses on diversity-productivity address only few of them. This approach has much potential, and I suggest it should be further explored in future studies.

Challenges for assessing the empirical relevance of hypothesized mechanisms

Causal network diagrams are helpful for explicitly describing or developing hypotheses about the activity of mechanisms, because they allow providing a visual step-by-step description of those causal relationships that are suggested to give rise to the phenomenon of interest. Assessing the empirical support for hypothesized mechanisms, however, is still a tricky task, at least in the field of invasion ecology (Heger et al. 2021). The following section will focus on two specific challenges, namely the unclear role of single empirical studies, and the difficulty of empirically clarifying the range of applicability of a mechanism.

Single empirical studies can usually only address parts of hypothesized mechanisms. If the aim is to test whether enemy release is driving invasion success, a decision needs to be made concerning what exactly the survey or experiment should focus on. A single greenhouse study could for example test whether less tissue damage leads to enhanced growth in a specific plant species. It would require a different setting and an additional experiment to test whether enhanced growth leads to an increase in competitive ability. Single case studies therefore do usually not allow making inferences about a 'full' complex mechanism like the enemy release hypothesis as depicted in Fig. 1c, and their role with respect to theory building is therefore not straightforward (Heger and Jeschke 2018a).

The approach suggested above, combining causal network diagrams with the HoH approach, allows clearly stating which part of a hypothesized causal network a specific case study addresses. Misleading generalizations, for example stating that a respective case study found evidence 'in favor of the enemy release hypothesis' without further indication of the specific section of the causal network that has been studied, could thus be avoided. Ideally, explicitly stating which mechanism, and which exact part of it is addressed with an empirical test would become part of the scientific workflow. One way to achieve this could be to incentivize the publication of fine-grained description of hypotheses and summaries of respective results of empirical tests as nanopublications (Kuhn et al. 2018). Another possibility would be to build an encompassing interactive online tool that maps existing hypotheses, for example based on the hi-knowledge tool introduced above (for a suggestion, see Jeschke et al. 2021), enriched with causal network diagrams providing fine-grained descriptions of hypothesized mechanisms. In the future, such a tool could allow for (pre-) registration of empirical tests and summary reports of respective results (Heger and Jeschke 2018a). Scientists could thus directly contribute with their research to a growing, detailed, visual summary of the evidence base for a respective hypothesis.

The implementation of such a tool or other novel approaches enhancing fine-grained reporting on mechanisms is for sure desirable. However, drawing conclusions about the empirical relevance of a hypothesized mechanisms would still remain challenging, since analyzing parts of a causal network in isolation may yield misleading results. Different segments of a causal network may be interlinked, and studying them in isolation may conceal their interactions. Also, the systems studied in invasion biology usually are causally heterogeneous, meaning that many different factors are potential causes for a phenomenon of interest (Elliott-Graves 2016). A single case study may thus have identified a causal factor relevant for the specific context represented in that study; but this may tell little about the significance of this same factor for a different context (Heger 2001). Complex causal network diagrams, depicting several potential causal factors within one graph, may help to at least clarify that the identified causal factor is one among many other potentially relevant factors (Schurz 2021).

Above, I suggested that describing a mechanism in ecology means to describe causal relationships plus their scope and extent. Causal network diagrams can help with describing causal relationships step by step; a remaining challenge still is to find out about their range of applicability. A promising way forward in this respect could be to utilize accumulating empirical evidence for identifying classes of cases with lower causal heterogeneity (Elliott-Graves 2016; Heger and Jeschke 2018a; Küffer et al. 2013). Causal heterogeneity at least partly stems from heterogeneity in the studied systems. For example, the high abundance of plant species in a specific area can be caused by an excess of nutrients in the soil. This specific factor will, however, not be a direct cause for high abundance of an invasive mammal in the same area; here, a likely cause will be high abundance of prey. Similarly, enemy release may be an explanatory mechanism for some, but not for all species, or in some, but not in all ecosystems. Focusing future research on identifying the range of applicability of hypothesized mechanisms will thus be of major importance for improving prediction and management.

A major practical challenge for determining the scope and extent of hypothesized mechanisms, however, is a lack of data. Even though the enemy release hypothesis is a very well-known hypothesis (Enders et al. 2018), the number of studies providing empirical data is still limited. In the review study introduced above, a rough categorization of study systems according to the three taxonomic groups of plants, invertebrates and vertebrates, or the three habitat types terrestrial, freshwater and marine did not deliver consistent results concerning the respective level of supporting evidence (Heger and Jeschke 2018b). It would be necessary to split the studies into finer grained groups, also taking a look at specific parts of a mechanism separately; but there will rarely be enough data allowing to assess the full causal network within one study system. In the data set used for that review, many empirical tests of the enemy release are available on terrestrial plants (119 tests); only three tests, however, are available concerning freshwater plants. Out of the total of 163 tests identified for that review, only four focus on enemy release in invertebrates; and none of these addresses the sub-hypotheses of enhanced performance in the invaded range (data from https://hi-knowledge.org/). It seems, therefore, that the identification of classes of cases with low causal heterogeneity can hardly be achieved with a data-driven approach. Instead, it might be more useful to choose a theory-driven path, using basic ecological knowledge to identify potentially homogeneous classes of cases. For example, some plant species produce chemical compounds toxic for many herbivores. In their native range, herbivores often evolved adaptations to cope with these chemicals. If those plants invade a new area where species producing these chemicals are missing, they will quite likely experience enemy release.

Conclusion

A major goal of this paper was to harness philosophical work on the concept of 'mechanism' for invasion biology, and to indicate the potential usefulness of representing mechanisms as causal network diagrams. Talking about 'mechanisms' is very common in invasion ecology and also in ecology in general, but I suggest that a more mindful usage of the term could enhance efficiency in research. For example, the difference between hypothesized correlational patterns and hypothesized causal mechanisms is often not made clear (Schurz 2021). According to the conception of mechanism introduced above, describing mechanisms means providing step-by-step descriptions of how recurring causal relationships give rise to a phenomenon of interest. My hope is that fine-grained descriptions of mechanisms, combined with visual representations as causal networks, will stimulate and enhance the in-depth study of the drivers of biological invasions. I suggest that this approach can be equally well applied in other areas of ecology. Improving the precision of argumentation could help refining research questions in any other ecological area as well. Adding visualizations in the form of causal network graphs to written work could enhance theory development, since it forces one to spell out hidden assumptions, thus revealing potential conceptual inconsistencies.

The second aim of this paper is to point to current challenges in using empirical findings for assessing the range of applicability of hypothesized mechanisms. Taken together, the suggestions provided above could help to address some of the respective challenges in invasion ecology. Other, major challenges remain, mainly due to the high complexity and causal heterogeneity of the study systems and subsequent practical limitations. It is obvious that invasion ecologists, and ecologists in other fields as well, will have to deal with patchy knowledge also in the future. This circumstance triggers questions. For example, under which circumstances can enemy release be regarded as a mechanistic explanation for a specific invasion under study? Is it necessary to provide supporting empirical evidence for every causal connection hypothesized in Fig. 1c? Under which circumstances can enemy release be regarded as a mechanistic explanation for a class of cases regarded as rather homogeneous? Can negative evidence be allowed to some degree, or would any empirical test questioning the existence of any causal link in the network necessarily lead to an exclusion of this case from the group? These questions in my point of view require future research, done jointly by ecologists and philosophers.

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Declarations

Conflict of interest The author declares that she has no conflicts of interest.

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